

# THE STOMACH ANATOMY OF SOME EASTERN NORTH AMERICAN MARGARITIFERIDAE (UNIONOIDA: UNIONACEA)

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## ABSTRACT

Previous investigations on the stomach anatomy of various unionacean species have revealed similarities to that of *Neotrigonia* sp., a member of the marine Trigonioida, a group believed ancestral to the Unionoida. The present study investigated the stomach anatomy of the most primitive unionacean family, the Margaritiferidae. The morphology of the margaritiferid stomach is variable and in some ways appears intermediate between trigonids and other unionaceans. The overall similarity of stomach morphology among trigonids, margaritiferids, and other unionaceans provides additional evidence of a phylogenetic relationship between the Trigonioida and Unionacea. Although distinct morphological patterns are present within *Margaritifera margaritifera*, *M. marrianae*, and *Cumberlandia monodonta*, none of these suggests anything greater than species-level differences.

The bivalve stomach has received considerable study (Purchon, 1977). Representative families of each subclass have been investigated and major morphological patterns of stomach anatomy have been demonstrated. However, disagreement exists as to the interpretation of various stomach morphologies in some groups (Purchon, 1958, 1960; Dinamani, 1967). Within the polysyringian (= eulamellibranch = synaptorhabdic) order Unionoida, superfamily Unionacea, stomach anatomies of the genera *Anodonta*, *Lamellidens*, and *Lampsilis* (Unionidae) and *Velesunio* (Hyriidae) have been studied (Gutheil, 1912; Graham, 1949; Owen, 1955; Purchon, 1958; Dinamani, 1967; Kat 1983a, b). The unionid stomach appears to be fairly uniform in morphology, and the stomach of the single hyriid form examined was similar to unionid species (Purchon, 1958). However, Kat (1983a, b) noted differences in the shape and relative proportions of stomach structures among species of the genera *Anodonta* and *Lampsilis*. Kat (1983a, b) further maintained that species groups within each genus could be diagnosed using stomach anatomy in conjunction with other morphological and non-morphological characters.

The anatomy of the stomach of the Margaritiferidae, the third presently recognized family in the Unionacea, is unknown. Other anatomical characters suggest that the Margaritiferidae is the most primitive group within the Unionoida (Ortmann, 1911; Heard, 1974; Smith, 1979). Fur-

thermore, the Margaritiferidae possess specific anatomical traits that link unionoids with marine Trigonioida (Gould and Jones, 1974; Smith, 1980; 1983). On the basis of shell characteristics the trigonioids have been implicated as the likely ancestral group to the unionoids (Cooke, 1927; Newell and Boyd, 1975). The present study was undertaken to determine if stomach anatomy would provide additional information on the relationships between the Margaritiferidae and other unionacean families and the Recent marine trigonids. It was hoped these investigations would also present a better understanding of the evolutionary and systematic relationships of the genera *Margaritifera* and *Cumberlandia*.

The stomach morphology of the following three representative species of the Margaritiferidae was examined: *Margaritifera margaritifera* (L.), a species occurring in eastern North America and Europe; *M. marrianae* Johnson, a species with a very restricted distribution in the Gulf coast region; and *Cumberlandia monodonta* (Say), a widely distributed species in east-central North America and one showing the greatest apparent morphological divergence among the more fully described margaritiferid species.

## MATERIALS AND METHODS

A total of 21 specimens representing the three margaritiferid species mentioned above were

dissected. Of these 41 specimens, six (*M. margaritifera*) were used for initial exploratory dissections and histological examination and were not included in the morphological analysis. All specimens dissected had been fixed in 10% formalin and stored in either 50% isopropyl alcohol or 70% ethyl alcohol. Specimens were preserved unrelaxed, or were preserved following freezing, or were relaxed prior to preservation. Methods of preservation, although influencing the shape of the stomach, did not affect the appearance of internal structures. All material relevant to this study, except for a few specimens that were loaned to me by Mr. Tom Freitag, is presently housed in the Invertebrate Division of the Museum of Zoology, University of Massachusetts, Amherst (UMA). The following list provides particulars of specimens used in this study.

*Margaritifera margaritifera*:

UMA MO. 683, MA, Hampshire County, Amherst, Cushman Brook, 3 September, 1974. Four specimens.

UMA MO. 1066, RI, Washington County, Exeter, Queen River, 25 August, 1978. Three specimens.

UMA MO. 1273, PA, Schuylkill County, Ryan, Locust Creek, 13 March, 1982 and 23 June, 1983. Five specimens.

UMA MO. 1347, MA, Hampden County, Palmer, Quaboag River, 20 October, 1982. Four specimens.

UMA uncataloged, MA, Hampshire County, Amherst, Fort River, 1 August, 1984. Three specimens.

*Margaritifera marrianae*:

UMA MO. 1248, AL, Crenshaw County, Rutledge, Horse Creek, 2 August, 1981. Six specimens.

*Cumberlandia monodonta*:

UMA MO. 1143, TN, Hawkins County, Kyles Ford, Clinch River, 7 and 12 August, 1979. Five specimens.

UMA MO. 1425 and T. Freitag (uncat.), MO, St. Louis County, Eureka, Meramec River, 28 October, 1982. Three specimens.

UMA MO. 1426, IL, Rock Island County, Rock Island, Mississippi River, 18 August, 1978. One specimen.

T. Freitag (uncat.), IA, Mercer County, Muscatine, Mississippi River, 19 June, 1978. One specimen.

In addition to the margaritifera specimens, four specimens of *Anodonta implicata* Say and a single specimen of *Lampsilis radiata* (Gmelin) were dissected for inspection of stomach floor morphology. These dissections were to familiarize myself with the structures and terminology discussed by Kat (1983a,b). These dissections were also used to compare with Kat's (1983a,b) observations and with my own dissections of margaritifera stomachs.

Stomachs and surrounding visceral tissue were removed from specimens. The isolated tissue containing the stomach was then dissected from the dorsal side (nearest to the hinge) and examined using a stereozoom binocular dissecting microscope. The areas of ciliated ridges lining the internal surfaces of the stomach were assumed to represent the "sorting areas" of previous investigators. No attempt was made to determine the function of the extensive ciliary systems (sorting areas) of stomachs of live animals. The term "sorting area" is used in subsequent descriptions to

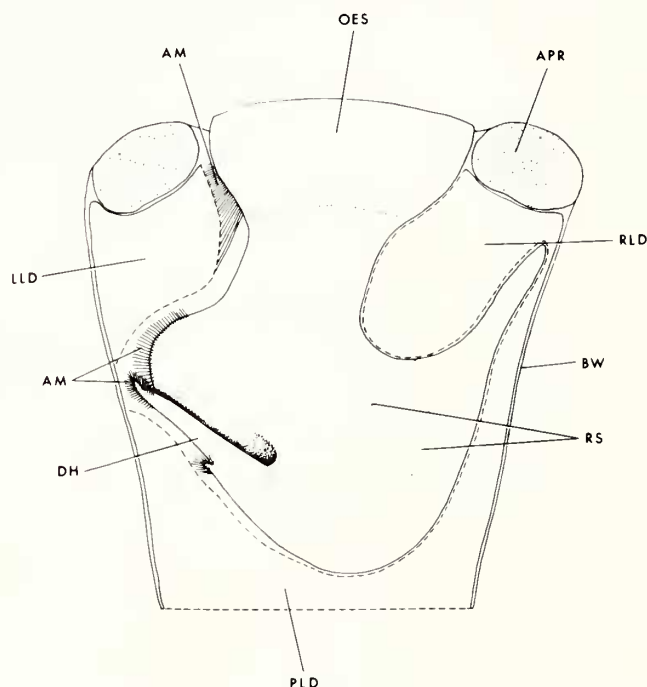
identify specific areas in which ciliated ridges are present.

The terminology of the various structures of the bivalve stomach has not been as consistent as that of other major organs of the pelecypod body. This is particularly true in the sorting areas covering the inner stomach surfaces. The situation will not be easily remedied, certainly not by proposing new terms. Therefore, this paper will follow, as closely as possible and where applicable, Purchon's (1958) terminology for *Anodonta cygnea* (L.).

## RESULTS

### GENERAL STOMACH ANATOMY

In the margaritifera species examined the stomach is situated dorsally and anteriorly in relation to the visceral mass. The general shape of the esophagus and stomach and the external morphology of the stomach roof is shown in figure 1. The stomach is an enlarged sac surrounded laterally and ventrally by digestive gland (LLD, RLD, PLD). Dorsally, the

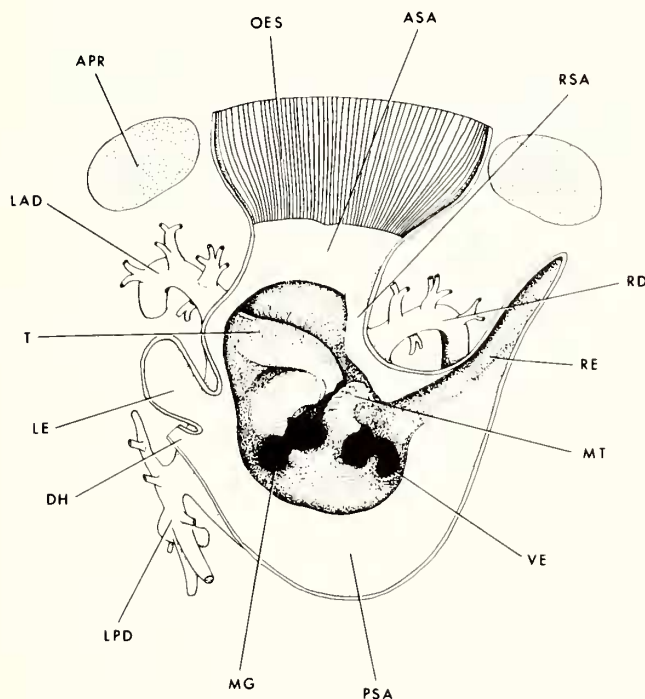


**Fig. 1.** The generalized roof of the margaritifera stomach and associated organs and structures. Dashed lines represent cuts in tissue. Abbreviations: AM = attachment muscle, APR = anterior pedal retractor muscle, BW = body wall, DH = dorsal hood, LLD = left lobe of digestive gland, OES = esophagus, PLD = posterior lobe of digestive gland, RLD = right lobe of digestive gland, RS = ridges delimiting principal sorting areas of roof. Horizontal field width = 13 mm.

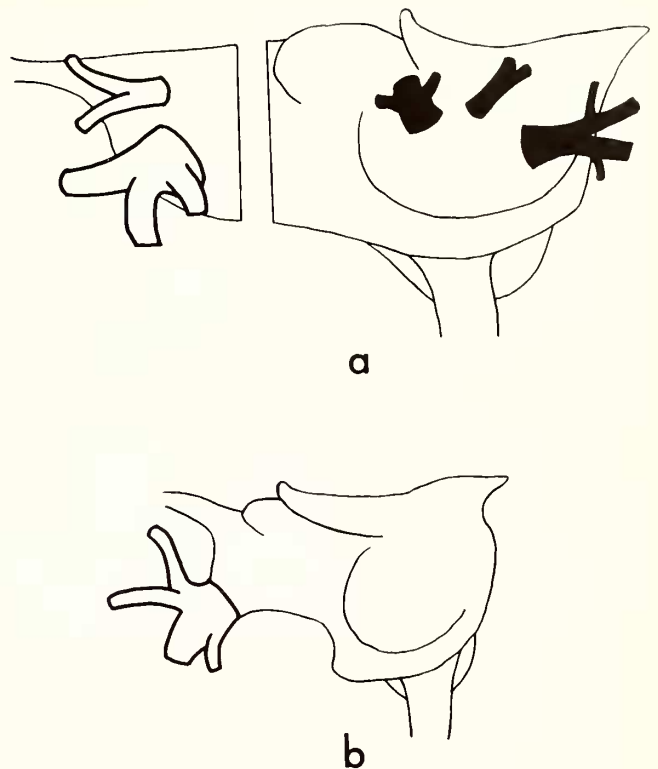
right and left lobes of the digestive gland extend over the roof but do not meet anteriorly. The esophagus (OES) is a flattened, short tube lying beneath the anterior adductor muscle and resting between and on the visceral muscles and the anterior muscles of the foot (APR). The lateral margins

of the esophagus are held in place by bands of attachment muscle (AM). The morphology of the stomach roof is in general agreement with other unionaceans (Graham, 1949; Purchon, 1958; Dinamani, 1967; Kat 1983a,b). The dorsal hood (DH) represents the most outstanding feature of the roof and is supported along with other portions of the left wall by attachment muscles (AM). Two prominent ridges (RS) are visible through the roof. These ridges delimit the principal sorting areas of the interior surface of the roof.

Internally (Fig. 2), the stomach floor, and in particular the lateral and posterior walls, are generally similar to other unionaceans. The gastric shield, not shown in the figure, shows no differences from *Anodonta* spp. (Graham, 1949; Purchon, 1958) or *Lamellidens* sp. (Dinamani, 1967). The same is true for the posterior wall and the left wall, with some exceptions depending upon the species investigated. The right embayment (RE) increases the area of the stomach. Ducts leading to the digestive diverticula originate from the anterior right and left walls (LAD, RD), and from a pocket in the left posterior wall (LPD) ventral and posterior to the dorsal hood (DH) and a shallow left embayment (LE). The right wall, particularly the right sorting area (RSA), combining the "longitudinal ridge" (Purchon, 1958) and the "anterior fold" (Dinamani, 1967), showed considerable variation



**Fig. 2.** Generalized interior and digestive duct systems of the margaritifera stomach. Abbreviations: APR = anterior pedal retractor muscle, ASA = anterior sorting area, DH = dorsal hood, LAD = left anterior duct system, LE = left embayment, LPD = left posterior duct system, MG = midgut and style sac, MT = minor typhlosole, OES = esophagus, PSA = posterior sorting area, RD = right duct system, RE = right embayment, RSA = right sorting area, T = major typhlosole, VE = ventral embayment. Horizontal field width = 13 mm.



**Fig. 3.** Diagrammatic representation of the left anterior (open, heavy lines) and posterior (solid) duct systems of the stomach showing maximum variation observed: a, composite of different specimens of *M. margaritifera*; b, specimen of *M. marrianae*. Horizontal field width = 17 mm.

among the species studied. The stomach floor contains a major typhlosole (T) which arises from the midgut (MG) and shows a strong fold and a swollen "conical mound" (Purchon, 1958) characteristic of other unionaceans at the apex of the fold. The typhlosole then proceeds to the left where it variously enters or terminates at the opening of the left anterior digestive duct system (LAD). The minor typhlosole (MT) arises near the major typhlosole and curves to the right posterior to the right digestive duct (RD). The ventral embayment (VE) is rather uniform throughout the species examined and represents a ventral extension of the posterior stomach floor. No comparison can be made with other unionacean species studied as this structure was not discussed by previous investigators. No consistent differences were detected between margaritifera species and the few unionid species examined in this study.

Anteriorly, the termination of the esophagus (OES) is marked by a rim, as is the case in other unionaceans. The area immediately posterior to the esophageal rim, the anterior sorting area (ASA), is variously developed in examined margaritifera species. The interior floor surface is covered with extensive sorting fields, which Purchon (1958) differentiated and identified. These sorting fields are associated with the typhlosoles, duct openings, and embayments. No special differences were noted between margaritifera species and other unionacean species previously studied.



## SPECIES DESCRIPTIONS

**MARGARITIFERA MARGARITIFERA.** The stomach of this species demonstrated the greatest dissimilarity with the typical unionacean stomach as described by previous investigators. Whereas in other unionaceans in which the major typhlosole always terminates well inside the left anterior duct opening, the major typhlosole in *M. margaritifera* did not consistently enter the duct system. This condition is somewhat dependent on the population studied. In individuals of one population sampled, the major typhlosole entered the duct. In contrast, in another population the organ terminated near the entrance of the duct. Furthermore, a few populations sampled contained animals in which both conditions existed.

The right duct system was always observed to arise from a single opening in the right wall of the stomach. The left anterior duct system usually arose from a single opening in the left wall, as in other unionaceans, except perhaps *Lamellidens* sp. (Dinamani, 1967), occasionally, two openings occurred (Fig. 3a). Posteriorly, the left posterior duct system commonly had a single opening, which branched into anterior

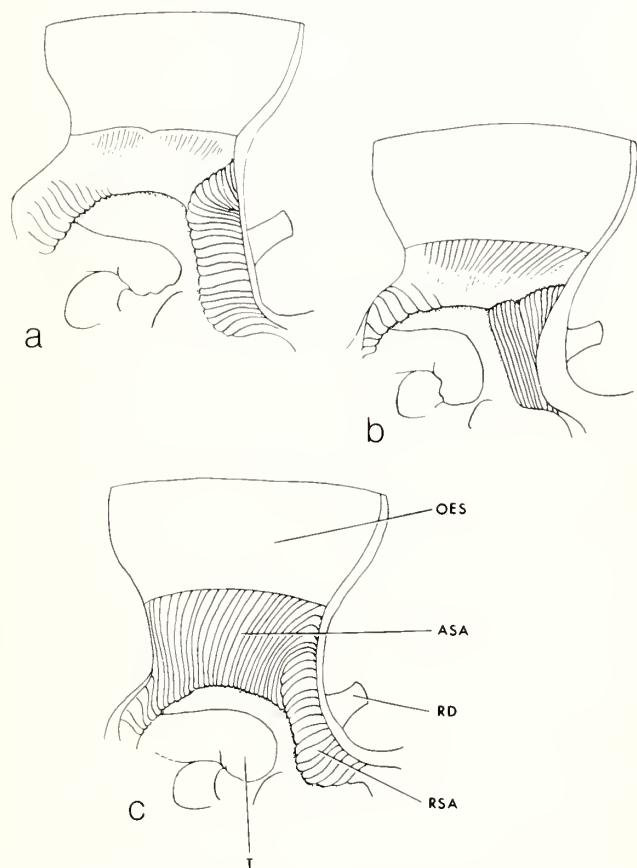


Fig. 4. Detail of the anterior and right side sorting areas of the stomach interior: a, *M. margaritifera*; b, *M. marrianae*; c, *C. monodonta*. Legend in c applies to a and b. Lines in sorting areas indicate orientation of ciliated ridges. Abbreviations: ASA = anterior sorting area, OES = esophagus, RD = right duct system, RSA = right sorting area. Horizontal field width = 7 mm.

and posterior trunks (see Fig. 2). Exceptions rarely occurred in which certain specimens showed multiple openings (Fig. 3a).

Sorting areas were variously developed along the right side and anterior floor of the stomach interior. The right side sorting area was a low shelf (Fig. 4a), not strongly set off from the anterior stomach floor as it is in some species of the unionid genera *Lampsilis* (Kat, 1983b) and *Anodonta* (Smith, pers. obser.). Purchon (1958) and Dinamani (1967) did not provide sufficiently detailed descriptions of the right sorting area to make comparisons with margaritiferids. The sorting ridges of the right sorting area extended anteriorly and medially from the right side wall. A weak sorting area, analogous (but not necessarily homologous) to "SA7" of Purchon (1958), was usually present, even if barely developed. The sorting area was occasionally absent altogether (Fig. 4a).

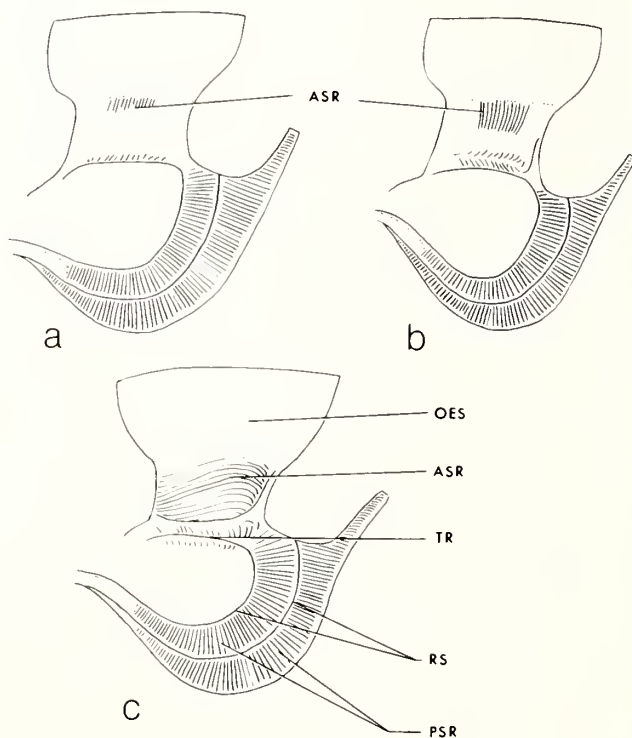


Fig. 5. Detail of the sorting areas of the stomach roof, as viewed through the roof: a, *M. margaritifera*; b, *M. marrianae*; c, *C. monodonta*. Legend in c applies to a and b. Lines in sorting areas indicate orientation of ciliated ridges. Abbreviations: ASR = anterior sorting area of roof, OES = esophagus, PSR = principal sorting areas of roof, RS = ridges delimiting principal sorting areas of roof, TR = transverse ridge. Horizontal field width = 9 mm.

The roof of the stomach contained the least developed sorting areas of all three species (Fig. 5a). The two principal posterior sorting areas (PSR, Fig. 5) of the roof were consistent with other investigated unionacean species. A poorly defined system of weak sorting ridges was sometimes present (ASR, Fig. 5a) anterior to a transverse ridge (TR, Fig. 5). The relationship of this sorting area to the anterior

sorting area of the roof in *A. cygnea* ("SA8," Purchon, 1958) is unknown. These small patches of sorting ridges in *M. margaritifera* were frequently absent.

**MARGARITIFERA MARRIANAE.** The stomach of this species showed characteristics more typical of unionaceans than did the stomach of *M. margaritifera*. The major typhlosole was always observed to enter the opening of the left anterior duct system. The right and left anterior duct systems each opened to the stomach interior through single large openings in the stomach wall. The left posterior duct system arose from a single duct opening. The ducts leading from the opening of the left posterior system were reduced in size and complexity when compared to those of *M. margaritifera*. Anterior branches were often lacking and in a single specimen the left posterior duct system was missing altogether (Fig. 3b).

Both the anterior and right side sorting areas were developed to a greater extent than in *M. margaritifera*. The anterior sorting area was always present (Fig. 4b), if not extensively developed. Sorting ridges extended posteriorly from the esophageal rim but dissipated after a short distance. The right sorting area was considerably developed beyond the condition found in *M. margaritifera*. The area existed as a raised anteriorly lobate shelf (Fig. 4b). Sorting ridges traversed the shelf parallel to the axis of the animal. The shelf did not come into contact with the ridges of the anterior sorting area.

The morphology and position of the sorting areas (Fig. 5b) of the roof anterior was similar to that of *M. margaritifera*. The only exception noted was that the sorting ridges of the transverse ridge and the anterior sorting area were well formed and consistently present.

**CUMBERLANDIA MONODONTA.** Among the three margaritiferid species examined, the stomach of *C. monodonta* most closely resembled that of other unionaceans. The major typhlosole consistently entered the large opening of the left anterior duct system. The right side duct system arose from a single opening in the right wall. The left anterior duct system usually opened to the stomach through a single opening, but occasionally two openings were present, as was the case in some *M. margaritifera* specimens (Fig. 3a). The left posterior duct system commonly had a single opening in the left posterior wall. In one specimen two openings occurred. Similar to *M. marrianae*, the left posterior duct system was reduced relative to the left anterior duct system. Although anterior branches were sometimes present in the posterior duct system, they were generally very reduced.

The right side and anterior sorting areas of the stomach floor were well developed (Fig. 4c). The anterior sorting area was as complete as that reported for any other unionacean species and was joined on its right side by the well defined system of ridges of the right side sorting area. Although not strongly differentiated from the anterior sorting area, the right side sorting area was otherwise similar to that of *M. margaritifera*.

Equally well developed were the sorting areas of the roof interior (Fig. 5c). The posterior sorting areas were typical

of the previous species discussed. Anteriorly, the transverse ridge increased in width as it crossed the roof from right to left and showed a well differentiated anterior border that appeared as a separate ridge. The anterior ridge was not seen in either *M. margaritifera* or *M. marrianae* (Fig. 5). Sorting ridges were prominent on the transverse ridge and, occasionally, posterior to it. A distinctive and extensive area of sorting ridges (ASR, Fig. 5c) occurred anterior to the thickened transverse ridge. Such sorting ridges coursed obliquely to the body axis and then curved sharply to the posterior on the right side.

## DISCUSSION

The stomach of the Margaritiferidae, as determined from examination of three characteristic species, best conforms with the modified Type IV category of Purchon (1958) and the Section IIIC category of Dinamani (1967). Such designations are of limited use, however, as ambiguities and discrepancies in their definitions exist. This is particularly evident in attempts by Purchon (1958) and Dinamani (1967) to identify with certainty the so-called "left pouch" and correlate this feature with the various duct systems which enter the unionacean stomach. Therefore, and until a comprehensive study can provide an adequate resolution, an assignment of the descriptive term "left pouch" to any of the left wall embayments of the margaritiferid stomach has been deferred. With respect to other characteristics of the margaritiferid stomach, certain comparisons can be made with *Neotrigonia* sp. as well as other unionaceans.

A major feature which differentiates the unionacean stomach from the trigonid stomach is the alleged consistent entrance of the major typhlosole into the opening of the left anterior digestive duct system in unionaceans (Graham, 1949; Purchon, 1958; Dinamani, 1967; Smith, pers. observ.). In *Neotrigonia* sp. the major typhlosole always terminates prior to reaching the left anterior duct opening (Purchon, 1957, 1958). Also, in unionaceans a sorting area on the anterior floor of the stomach immediately posterior to the terminus of the esophagus ("SA7") is purportedly present (Purchon, 1958; Dinamani, 1967; Kat, 1983a,b; Smith, pers. obser.) whereas in *Neotrigonia* sp. it is absent (Purchon, 1957, 1958). However, in some specimens of *M. margaritifera* the major typhlosole terminates prior to the left anterior duct system opening. Furthermore, specimens of *M. margaritifera* often lack an anterior sorting area on the floor ("SA7") posterior to the esophagus. The observed variation in margaritiferid species could be merely indicative of wider variation in margaritiferids or suggestive of an intermediate condition between unionaceans and trigonids.

Relating the digestive duct systems of the examined margaritiferid species to both trigonids and other unionaceans is more difficult. The most simple form is apparently expressed by *Neotrigonia* sp. In this genus three distinct openings of the digestive duct system occur in the stomach wall, two anterior on either side of the esophageal opening and one on the left posterior wall (Purchon, 1957). The digestive duct openings of the described unionacean species vary



somewhat from the trigonid condition. Both Purchon (1958) and Dinamani (1967) have described additional duct openings in the unionacean species they examined. Kat (1983a,b), other than noting the location of the two anterior duct systems, provided no specific information on the digestive duct system or the arrangement of duct openings. Therefore, unfortunately, no detailed comparisons can be made concerning the variation of duct system morphology between *Neotrigonia* sp., margaritiferids, and the many unionid species examined by Kat (1983a,b). However, based on Purchon's (1958) and Dinamani's (1967) observations, and assuming Purchon's (1957) description of *Neotrigonia* sp. is representative of the Trigonioidea, the unionaceans appear to demonstrate an increase in the complexity of the digestive duct systems. This suggestion is strengthened by observations presented in this paper on the morphology and variation of the digestive duct systems in margaritiferids.

Besides the few differences between the unionaceans and the trigonids, as revealed by Purchon (1958) and the discussion above, the stomach anatomies of trigonids and unionaceans are very similar. Such strong similarity provides additional evidence for claiming a monophyletic evolution of the Unionacea and a common ancestry between the Unionacea and the Trigonioidea. Such a close relationship, involving stomach and mantle anatomy and shell characteristics, has been recently expressed in a proposed revision of ordinal groups of the Pelecypoda (Nevesskaya et al., 1971) in which trigonoids and unionoids are placed in a single suborder Trigoniina. It must be pointed out, however, that significant differences between the two groups in larval morphology and biology, gill morphology, and adult biology not discussed by Nevesskaya et al., (1971) make unwise a reduction of the orders Unionoidea and Trigonioidea to a common suborder.

Using stomach anatomy to evaluate relationships between the margaritiferids and other unionacean families offers little basis for new insight. Too few unionids, hyriids, and margaritiferids have been examined or studied in detail to draw conclusions about family-specific characteristics of the various sorting and duct systems of each group. No significant differences exist in the structure of the typhlosoles or the positions of the major sorting areas. It may be that the general structure of the stomach, like other internal organs, was laid down in the most primitive ancestral unionoid and has remained essentially constant in subsequently evolved groups.

The genus *Cumberlandia*, and its relationship to the genus *Margaritifera*, has received recent attention by Davis and Fuller (1981). They concluded that the similarity of genetic distances exhibited by all margaritiferid species they examined (including *C. monodonta*) did not justify generic distinction of *Cumberlandia*. The present study provides some support for Davis and Fuller's (1981) contention. The overall morphology of the stomach of *C. monodonta* shows no greater divergence than does that of *M. marrianae* from the stomach of *M. margaritifera*, the most likely ancestor to both species (Walker, 1910). Although the anterior and roof sorting systems are most developed in *C. monodonta* (Figs. 4 and 5), there

is less difference in the right side sorting area when compared to *M. marrianae* (Fig. 4). The right side sorting area of *M. marrianae* is well developed and completely unlike that of *M. margaritifera* and *C. monodonta* which have similar right side sorting areas. Furthermore, the reduction of the posterior digestive duct system in both *C. monodonta* and *M. marrianae* might be indicative of a trend in two closely related species to reduce the number of ducts communicating between the stomach and the digestive gland. Because of other yet unresolved questions regarding the anatomy of *C. monodonta*, it would be premature to reduce the genus *Cumberlandia* to a lower taxonomic category. Beyond general anatomical work, additional studies on larval morphology and biology, marsupial gill morphology (during incubation periods), and gill support structures in other margaritiferid species must be performed before further revision is justified.

## ACKNOWLEDGEMENTS

I should like to thank Mr. Tom Freitag for supplying specimens of *Cumberlandia monodonta* for study. I also thank Dr. Kenneth J. Boss for reading an earlier draft of this paper.

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